"I have lived to see state after state extirpate its wolves. I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anaemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddlehorn... I now suspect that just as a deer lives in mortal fear of its wolves, so does a mountain live in mortal fear of its deer. And perhaps with better cause, for while a buck pulled down by wolves can be replaced in two or three years, a range pulled down by too many deer may fail of replacement in as many decades."

Aldo Leopold (1948), A Sand County Almanac

"It is of course too late to salvage more than a lopsided system of wilderness study areas, and most of these remnants are far too small to retain their normality in all respects. Even the national parks, which run up to a million acres each in size, have not been large enough to retain their natural predators, or to exclude animal diseases carried by livestock. Thus the Yellowstone has lost its' wolves and cougars, with the result that elk are ruining the flora, particularly on the winter range."

Aldo Leopold (1948), A Sand County Almanac

University of Alberta

Wolves, elk and willow on Yellowstone National Park's northern range.

by

Hawthorne L. Beyer

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Master of Science*

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring 2006

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This work is dedicated to my brother, Trevelyan

ABSTRACT

Reintroduction of wolves (*Canis lupus*) to Yellowstone National Park in 1995–96 has been argued to promote a trophic cascade by altering elk density, habitat-selection patterns, and behaviour that, in turn, could lead to changes in the plant communities used by elk (*Cervus elaphus*). I studied two species of willow (*Salix boothii* and *S. geyeriana*) on the northern range to determine whether 1) there was quantitative evidence of increased willow growth following wolf reintroduction, 2) browsing by elk affected willow growth, and 3) the increase in growth observed was greater than that expected by climatic and hydrological factors alone, thereby indicating a trophic cascade caused by wolves. I then adopted a movement modeling approach to examine whether a behavioural response of elk to wolves could result in reduced browsing of willow. I conclude that a behaviourally mediated trophic cascade between wolves, elk and willow is occurring on the northern range.

ACKNOWLEDGEMENTS

Many people have collaborated with me on this work. I thank Evelyn Merrill and Mark Boyce for their valuable insight, guidance, encouragement, and the fertile academic environment they have worked hard to create at the University of Alberta. I value extremely the time I have spent discussing ecology with my friends and peers: Daniel Fortin, Jacqui Frair, James Forester, Scott Neilson, Mark Hebblewhite, Cam Aldridge, Darcy Visscher, Carrie Roever, Dean Anderson, Juan Morales, Dan Haydon and Nathan Varley. I thank you all for your advice and assistance – I leave here a smarter man for having known you. I also particularly wish to thank my collaborators at Yellowstone National Park for their valuable support, especially Doug W. Smith, P.J. White, Glenn Plumb, and Christie Hendrix.

Funding for this research was provided by The National Geographic Society and The National Science Foundation (Grant No. 0078130). Additional support was provided by the National Park Service and the Alberta Conservation Association.

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CHAPTER 1

GENERAL INTRODUCTION

Trophic cascades occur when predators affect lower trophic levels via their influence on one or more intermediate trophic levels. They are important because they are fundamental to our understanding of *how ecosystems are structured*. Top predators can have a profound influence on lower trophic levels of an ecosystem (Leopold 1948) and these "top down" effects are thought to play an important role in maintaining ecosystem stability and diversity (Paine 1980). Developing a mechanistic understanding of these processes that maintain healthy ecosystems is critical if we are to make informed management decisions and effectively direct conservation efforts.

One of the most striking examples of the importance of top predators in maintaining ecosystem processes is that of sea otters (*Enhydra lutris*), their prey, sea urchins (*Strongylocentrotus* spp.), and kelp (e.g. *Laminaria groenlandica*) on the Pacific Coast of North America (Estes & Duggins 1995). Extirpation of sea otters by humans allowed the urchin population to grow large. Increased grazing activity of the urchins resulted in the widespread removal of kelp, which had provided primary habitat for many species of fish and invertebrates. Thus the loss of kelp resulted in a profound loss of biomass and diversity in this marine ecosystem. Restoration of the sea otter through conservation efforts re-established the processes and mechanisms that maintained the stability of the ecosystem, and effectively restored the community to its' former state.

A parallel situation may exist in Yellowstone National Park. Until the reintroduction of wolves (*Canis lupus*) in 1995 and 1996 (Bangs and Fritts 1996) Yellowstone National Park had been without wolves for about 70 years, their extirpation

due to predator-control efforts in early park management (Weaver 1978). The restoration of wolves has been hypothesized to promote a trophic cascade by altering prey habitat selection patterns and behaviour that, in turn, will lead to changes in plant community structure used by their prey (McLaren and Peterson 1994, Lima 1998, Berger et al. 2001, Smith et al. 2003).

In this thesis I examine evidence that a trophic cascade is occurring on Yellowstone's northern range between wolves, elk (*Cervus elaphus*) and willow (*Salix* spp.). To demonstrate that a trophic cascade is occurring, one must provide evidence that a) willow growth has increased since wolf reintroduction, b) that abiotic factors like weather, topography and groundwater do not account for this increase in growth, c) that elk browse negatively affects willow growth, and d) that the influence of wolves on elk has resulted in reduction in willow browse. In Chapter 2 I quantify willow growth pre- and post-wolf reintroduction using willow growth ring analysis, and evaluate whether an increase in willow growth has occurred above and beyond that expected from abiotic factors alone. I also examine the influence of browse on willow growth, which is important because it establishes a mechanism by which wolves could influence willow growth via their influence on elk. In Chapter 3 I adopt an elk-movement modelling approach to examine evidence that the behavioural response of elk to wolves could results in reduced browsing of willow. General conclusions that arise from this work are summarized in Chapter 4.

Both Chapter 2 and Chapter 3 are being submitted for publication in peer-reviewed journals. Chapter 2 will be submitted to *Ecological Applications*, and Chapter 3 will be submitted to the *Journal of Animal Ecology*.

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CHAPTER 2

WILLOW ON YELLOWSTONE'S NORTHERN RANGE: EVIDENCE FOR A TROPHIC CASCADE IN A LARGE MAMMALIAN PREDATOR-PREY SYSTEM?

2.1 INTRODUCTION

Since 1968, the ecological communities of Yellowstone National Park have been managed under a natural-regulation paradigm (Singer et al. 1998, Huff and Varley 1999). Natural regulation also has been described as "ecological-process management" (Boyce 1991) referring to the practice of allowing natural ecological processes to function with minimal human interference. Management of Yellowstone and other national park ecosystems under this paradigm has lead to debates over management of park resources (Boyce 1998, Peterson 1999, National Research Council 2002). One assertion is that Yellowstone's elk (*Cervus elaphus*) population was limited largely by winter severity, forage production, and density-dependent processes prior to wolf (*Canis lupus*) recovery, and the population was in dynamic equilibrium (Merrill and Boyce 1991, Coughenour and Singer 1996, Singer et al. 1998, Taper and Gogan 2002). However, concerns have been expressed that under natural regulation high herbivore densities have altered plant communities (Yellowstone National Park 1997, National Research Council 2002). While evidence suggests grassland communities experienced enhanced productivity with herbivory (Frank and McNaughton 1993), some woody plant communities may be suppressed under high browsing pressure (Singer et al. 1994, Wagner et al. 1995, Kay 1998). In fact, based on photographic evidence, the area of willow (*Salix* spp.) communities has declined by approximately 50%-60% since the early 1900's (Chadde and Kay 1991, Soulé et al. 2003) amounting to 0.4-0.8% of the park (Houston 1982).

Declines in willow may be attributed to a number of factors, but high ungulate densities, particularly elk, have been cited as the principal cause (Chadde and Kay 1991, Wagner et al. 1995, Kay 1998). Alternatively, willow declines may be a result of plant stress associated with changes in climate and/or hydrology (Houston 1982, Singer et al. 1994, Romme et al. 1995). Lowered water tables may have resulted from lower precipitation and run-off, higher temperatures, and reduced back flow due to the loss of beaver (*Castor canadensis*) populations (Singer 1996). Indeed, climatic records indicate an increase in mean summer temperature of 0.01 $^{\circ}C\ y^{-1}$, a decline in the Palmer drought severity index (representing a trend towards increased aridity) of $-0.019\ y^{-1}$ and a decline in mean winter precipitation levels of $-0.67mm\ y^{-1}$ during the past century (Balling et al. 1992). Most of the observed decline in willow arguably occurred during an extended drought in the 1930's (Houston 1982, Singer 1996) when elk numbers were unknown, but believed to be less than at present (Houston 1982).

In addition to allowing ecological processes to regulate populations, the natural-regulation paradigm directs managers to restore ecological processes that have been altered or lost through human actions. In particular, restoration of top predators is necessary for the functioning of trophic relationships (Soulé et al. 2003, Ray et al. 2005). Until the reintroduction of 14 wolves in 1995 (Bangs and Fritts 1996) Yellowstone National Park had been without wolves for about 70 years, their extirpation due to predator-control efforts in early park management (Weaver 1978). At least 174 wolves currently occupy the entire northern range (Smith et al., 2004b).

Reintroduction of wolves has been hypothesized to promote a trophic cascade by altering prey habitat selection patterns and behaviour that, in turn, will lead to changes in

plant community structure used by their prey (McLaren and Peterson 1994, Lima 1998, Berger et al. 2001, Smith et al. 2003). Although once thought to be uncommon in terrestrial systems (Strong 1992, Polis and Strong 1996, Lima 1998), recent evidence suggests that trophic cascading of carnivore effects on plants through their prey can be as significant in terrestrial systems as in other systems (Schmitz et al. 2000, Croll et al. 2005). Preliminary evidence indicates that wolves in Yellowstone National Park already may have induced changes in biomass accumulation and persistence of aspen (*Populus tremuloides*,) and cottonwood (*Populus* spp.) (Ripple et al. 2001, Beschta 2003).

In this paper, we evaluate the evidence for a trophic cascade between wolves, elk and willow. If a cascade has occurred since wolf reintroduction, we would expect to find evidence for a decrease in browsing on willow after wolf reintroduction compared to prior to wolf reintroduction, and an increase in willow growth in response to the release in browsing pressure. However, because browsing pressure has not been monitored consistently pre- and post-wolf reintroduction, we can address the growth release of willow from browsing only indirectly. As a result, we suggest evidence for a trophic cascade is demonstrated by (1) willow growth increasing when browsing is reduced, (2) willow growth being greater after than before wolf reintroduction, and (3) that the increase in willow growth after wolf reintroduction being greater than would be expected by alternative effects of climatic or hydrological factors.

2.2 METHODS

2.2.1 STUDY AREA

This study was conducted on the Yellowstone National Park's northern range (Wyoming, USA; 110° 23' W, 44° 55' N), a 1,526 km^2 area characterized by low elevation (1,500–2,000 m) grassland (*Festuca idahoensis*) and sagebrush (*Artemisia* spp.) grasslands fringed by coniferous forests (primarily *Psuedotsuga menzeseii, Picea engelmanni* and *Pinus contorta*) and scattered aspen (*Populus tremuloides*) stands (Despain 1990). Average annual precipitation on the northern range ranges from 25.1cm (Gardiner, MT) to 42.2 cm (Tower Falls, WY), with mean daily temperatures in Tower Falls of –10.4°C in January and 14.7°C in July (Western Regional Climate Center, Reno, Nevada, USA).

Sampling sites were located in the Blacktail, Oxbow, Geode, Slough, Lamar, and Soda Butte drainages (Figure 1.1) at elevations ranging from 1840-2240 m. Drainage bottom vegetation commonly consists of a mixture of sedges and grasses (*Carex* spp., *Deschampsia cespitosa, Calamagrostis canadensis*), forbs and shrubs (see Despain 1990 for a description of vegetation). The drainages range from broad floodplains up to 1-km wide (e.g. Lamar, Slough) to narrow, steep-walled gullies only a few meters wide (e.g. portions of Blacktail, Geode). On the sloped, upper reaches of drainages willow tends to occur only in close proximity (within rooting distance) of the stream, but can be widely distributed across the flat, wetter floodplains. This study focused on the two most common species of willow, *Salix geyeriana* and *S. boothii*, which can grow 4 m tall, although most willow clumps are much shorter due to heavy winter browsing by elk (Singer et al. 1994).

The wolf population has increased steadily since its reintroduction in 1995 with a current population of 174 wolves in 8 packs on the northern range (Smith et al. 2004b). While individual pack boundaries and sizes are dynamic, there has been a continuous presence of wolves on the northern range since their reintroduction (Smith et al 2003). Annual minimum convex polygon home ranges for each of the wolf packs (Smith et al. 2004b) indicate that most of the northern range has fallen within a wolf territory in all years since reintroduction. Elk numbers prior to wolf reintroduction varied from a low of 3,172 in 1968 to a high of 19,045 in 1994, and have declined by 4.5% yr^{-1} since the reintroduction of wolves. During winter, large herds of elk congregate in the valleys and foothills of the northern range (Houston 1982), while during summer elk typically move to higher elevations in the park (Mao et al. 2005). Elk are the principal prey for wolves, constituting 83% of their annual diet (Smith et al. 2004a). Moose (*Alces alces*) numbers on the northern range were at a high in 1970, but following the wildfires of 1988 moose became scarce and do not share winter range with elk on the northern range (Tyers and Irby 1995). Pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) also migrate to winter ranges that usually do not overlap the elk winter range (Barmore 2003).

2.2.2 SITE SELECTION AND WILLOW SAMPLING

We conducted initial reconnaissance of willow distribution on the northern range from a fixed-wing aircraft in July 2001 prior to selecting 30 possible sites at which *S. boothii* or *S. geyeriana* grew and that were at least 500m apart. At each of the 18 sites at which one or both species grew, we established a 25-m transect oriented parallel to the

stream passing through the center of the densest willow patches. At 1-m intervals along that transect we selected the closest individual willow clumps for sampling, with an individual willow clump defined as a cluster of stems emerging from the ground in close enough proximity to suggest they originated from the same root system. Within the clumps we selected a representative living stem and recorded the species, growth form (Keigley et al., 2003), and stem height from base of stem to tallest point of previous and current-year growth. Growth forms included stems that were arrested (intense browsing throughout life of stem that restricted height to 30-100cm), uninterrupted (browsing was evident but the stem gained height each year), or released (stems formerly arrested, but subsequently gained height after browsing intensity decreased) (Keigley et al. 2003). We recorded percent of twigs browsed on a stem as an index to browsing pressure by counting the number of browsed and unbrowsed twigs from the previous year's growth (Y_{t-1}), or second year's growth (Y_{t-2}). A 10-cm sample of the basal portion of each stem was cut at ground level, wrapped in protective paper, marked with a unique identification number, and transported to the lab for sectioning. If the stem growth form was released, a second segment of stem was collected from just above the arrest level to determine year of release. When less than 10 stems per species per growth form had been collected by the end of the transect, additional stems were sampled at regular intervals along the transect to ensure at least 10 stems were collected.

Stem sectioning and growth-ring measurement

The basal end of each stem segment was sanded using fine-grit sandpaper and the stem was soaked in water for at least 10 minutes, which softened the wood thereby

making it easier to section. Stem sections (22-28 μm thick) were cut with a microtome until one complete, evenly cut section was obtained. The section was soaked in distilled water for 2-3 minutes to ensure similar levels of hydration among all sections prior to mounting the section on a microscope slide. The section was then fixed in one drop of aqueous mounting fluid, covered with a cover slip, and sealed with nail polish. Slides were placed on a backlit stage and photographed with a Nikon digital camera attached to a 20x light microscope. A stage micrometer marked to 0.1mm was placed on top of the section prior to taking the image to provide a scale reference for ring measurements.

Ring widths were digitized from the images using custom software developed for ArcGIS (Environmental Systems Research Institute, 2004). Absolute ring area (mm^2) of each growth ring was estimated from a minimum of 4 ring widths taken at approximately equal intervals around the circumference of the ring. When the ring approximated a circle (82%), their area was calculated based the ring radius (pr^2) measured from the center to the outer ring edge *minus* the area of the circle calculated with a radius measured to the inner edge of the ring. When a ring was elliptical (6%), the same approach was used based on the area of an ellipse, plw, where l is half the diameter of the ellipse along the longest axis, and w is half the diameter of the ellipse along the shortest (perpendicular) axis. Ring areas of irregularly shaped stems (12%) were processed on a case-by-case basis using the previous approach but adding or subtracting an area that corresponded to the deviations of the irregularly shaped ring.

Site variables

To develop models to explain variation in annual ring growth, we derived yearly estimates (1989 to 2001) for 5 climatic factors that influenced growing-season conditions, 2 hydrological indices that relate to ground water, and previous winter maximum snow depth, which might have mediated browsing pressure. The five climatic variables were the same across all sites within a year, but all other variables were calculated on a per site basis. Total annual precipitation (PRECIPA; cm), and total growing season precipitation (May-August; PRECIPS) were from the Tower Falls Station (ID# 489025). The Palmer Drought Severity Index (PDSI; Wyoming Division 1, NOAA) is based on temperature and precipitation records and indicates prolonged moisture deficiency or excess. The North Pacific Index (NPI) was used as an index of climatic conditions because NPI has been found to predict local ecological processes better than local weather variables (see Hallett et al. 2004, Stenseth & Mysterud 2005). Average NPI was calculated for both the growing season (May-August; NPIS) and winter period (September-April; NPIW). Local climate conditions are influenced by elevation (ELEV), which was obtained for each of the sites from a 30m USGS digital elevation model.

Ground water table level is the hydrological variable that may have the most direct link to willow growth (Singer et al 2003), but because it is not consistently monitored in our study area, we used watershed area and stream flow rate as proxies. We averaged monthly stream flow rates on the Lamar River gauging station (USGS ID# 06187950) for May–August of each year. The extent of the watershed above each site

was calculated using watershed modeling software (ArcInfo; Environmental Systems Research Institute, 2004) and a 30m USGS digital elevation model.

Weekly estimates of snow depth (cm) from 1 January to 28 February 1985 to 2001 were predicted for each of our sites based on elevation, precipitation, topography, and vegetation using the spatial snow model (version 1) of Coughenour and Singer (1996) and averaged to provide an annual estimate of snow depth at each site for each year of the study.

Elk and Wolf Populations

We used the winter counts of elk on the northern range (ELK) to reflect potential browsing pressure the previous winter (White & Garrott 2005). The presence or absence of wolves was indicated as a binary variable in our analysis (WOLF): wolves were considered absent until winter 1996. Although wolves were reintroduced in the spring of 1995, the earliest they could have influenced willow browse would have been winter 1995-1996. Thus growth during summer 1996 would be the earliest that release in willow could be expected to occur.

2.2.3 DATA ANALYSIS

We followed a model-selection approach (Burnham and Anderson 2002) using Akaike's information criterion (AIC) to examine evidence that willow growth (ring area) in 2001 was related to browsing pressure (% browsed twigs/stem; PBRWS) in the winter preceding ring growth. We also hypothesized that site variables, including elevation, extent of watershed, and snow depth would influence willow growth and included these

variables in a set of 6 *a priori* models. We used a mixed-effects model with site as a random effect to account for the lack of independence of stems within a site. We included ring area from the previous years' growth (PYRA) to account for the fact that previous growth could influence growth the following year. Model selection was conducted for the two willow species separately.

To establish whether willow growth was greater following wolf reintroduction we compared the mean ring area for each willow species at the same site across the pre- and post-wolf reintroduction periods using a paired t-test with Bonferroni correction. Ring area was natural log transformed to create a normal distribution of values.

We also used model selection to compare competing models explaining variation in annual willow growth during 1989-2001 with and without a wolf effect. We first selected the best model for predicting willow growth based on climatic condition, winter snow depth, and hydrology and then tested the whether the inclusion of the presence of wolves improved the model fit (i.e., lower AIC). We again used a mixed-effects model framework with the random effect of stems nested within sites to account for the fact that rings within stems and stems within sites cannot be considered independent. Furthermore, because annual ring areas within an individual stem were autocorrelated in time (Pearson's r, lag = 1, *S. boothii*: = 0.707, *S. geyeriana* = 0.624), we used a first-order autoregressive structure, which assumed an exponential decrease in autocorrelation as lag increases. Model selection was conducted for the two willow species separately.

All statistical analyses were performed in R (R Development Core Team, 2004) using the "lme" function in the "nlme" library (Pinheiro and Bates 2000). The restricted maximum likelihood estimator (REML) was used in all models.

2.3 RESULTS

Ring area and browsing of previous- and second-year twigs were measured on 214 stems of *S. boothii* across 16 sites, and 115 stems of *S. geyeriana* across 7 sites (Figure 1.1). Percent of twigs browsed across sites ranged from 0-100 with a median of 100% for both species. In the 3 best models for both species (Table 1.1) we found evidence that willow ring growth in 2001 was positively related to ring growth in the previous year (*S. boothii*: ß = 0.6641 ± 0.0508 SE; *S. geyeriana*: ß = 0.6184 ± 0.0715 SE) and was inversely related to percent of twigs browsed on the stem in the winter preceding growth (*S. boothii*: ß = -0.2245 ± 0.0704 SE; *S. geyeriana*: ß = -0.4173 ± 0.1094 SE).

Annual ring areas were measured on 275 stems of *S. boothii* across 17 sites and 145 stems of *S. geyeriana* across 8 sites (Figure 1.1) for a total of 1,948 annual ring measurements. Ring counts indicated that the oldest stems were established in 1989. Because annual ring areas were on average smaller (t-test with Bonferroni correction, $P < 0.01$ for all comparisons with first-year stem areas) in the first year of growth (Figure 1.2) we excluded ring widths representing the year of establishment so this did not confound environmental effects. For both species, mean annual ring area in the 6 years following wolf reintroduction in 1995 was approximately two-fold higher (*S. boothii*: $t = -5.355$, df = 11, $P = 0.0002$; *S. geyeriana*: $t = -3.201$, df = 6, $P = 0.02$) than in the 4 (*S. boothii*) or 7 (*S. geyeriana*) years prior to wolf introduction (Figure 1.3).

Of the highest ranking models we evaluated to explain annual variation in willow ring area (Table 1.2), for *S. boothii* the model with the most support indicated that ring growth was inversely related to elevation (ß = -0.0017 ± 0.0004 SE) and mean annual precipitation (ß = -0.26 ± 0.02 SE), and was positively related to winter NPI (ß = 0.104 ±

0.04 SE) and wolf presence (ß = 0.33 ± 0.066 SE). For *S. geyeriana* the model with the most support indicated similar relationships with elevation (ß = -0.005 ± 0.0006 SE), winter NPI (ß = 0.09 ± 0.016 SE) and wolf presence (ß = 0.33 ± 0.066 SE), but mean annual precipitation was not included in the model (Table 1.2).

2.4 DISCUSSION

Our results provide direct evidence that browsing can reduce willow growth. Low levels of browsing can enhance productivity through stimulation of branching, flowering, and new shoot propagation (Wolff 1978, Elmqvist et al. 1987, Alstad et al. 1999, Singer et al. 2003) but long-term and severe browsing suppresses willow growth, flowering, and seed production (Bryant et al. 1983, Singer et al. 1994, Case & Kauffman 1997, Brookshire et al. 2002, Singer 1996). Browsing may negatively affect growth by reducing root carbon reserves, which would otherwise be used for the production of chemical defenses (tannins) and for future growth (Bryant et al. 1983, Wagner et al. 1995, Peinetti et al. 2001, Brookshire et al. 2002), and prevents plants from growing tall, thereby escaping herbivory. This creates the potential for a positive feedback loop (Rømme et al. 1995, Peinetti et al. 2001) whereby browsing ensures plants are short and therefore accessible, while also being more palatable due to reduced chemical defenses (Singer et al. 1994), resulting in continued browsing. The inverse relationship between browsing intensity and stem growth is central to the trophic cascade hypothesis as it establishes the mechanism by which a trophic cascade occurs: a reduction in browsing intensity can result in increased willow growth, leading to escape from herbivory if plants grow tall.

We also demonstrate an increase in the growth of willow on the northern range that coincides with the reintroduction of wolves. After accounting for climate and hydrology-related factors, the presence of wolves on the northern range was a significant predictor of willow growth in the highest ranked models for both willow species. Wolves may influence willow growth through direct and indirect effects. Although there is some evidence that predation may have reduced the elk herd (White & Garrott 2005), elk densities on the northern range ranged from 7.8 to 12.6 elk/km^2 during this study, densities at least eight times higher than the maximum density White et al. (1998) suggested would result in release of aspen in Banff National Park. We also found that elk population size was a predictor of willow growth, which further supports the hypothesis that the increase in willow growth we observed is caused by indirect and not direct effects of wolves on elk.

A trophic cascade between wolves, elk and willow could be mediated by indirect (behavioural) effects if elk distribution and/or foraging behaviour is altered by predation risk, thereby creating local refugia for willow in which browsing intensity is reduced and plant growth increases. Thus, to demonstrate indirect effects are mediating a trophic cascade evidence must be provided of two mechanisms: 1) that wolves alter elk distribution or feeding behaviour, and 2) that these behavioural responses result in reduce browsing of willow and therefore increased growth. There is evidence suggesting both of these mechanisms occur on the northern range. Ripple & Beschta (2003) compared browsing rates of cottonwoods at sites on the northern range and classified as high- or low-risk based on wolf detection potential and the presence of barriers to movement that would impede escape. They found that browse rates were lower, and plant heights were

higher, at the high-risk sites, and they attribute this to elk avoiding areas where susceptibility of wolves may be greater (Ripple & Beschta 2003). Indeed, wolves appear to be more successful at making kills at hard edges (forest edges and riparian areas) (Bergman et al. 2005), in ravines, close to water, and on ice (Kunkel & Pletscher 2000, Kunkel & Pletscher 2001) probably as a result of decreased speed, maneuverability and escape routes in these areas (Bergman et al. 2005). There is also evidence that elk alter their habitat selection in response to wolf density (Creel et al. 2005, Fortin et al. 2005). In a study of elk movement on the northern range post-wolf reintroduction, Fortin et al. (2005) demonstrate that habitat selection by elk changed in response to wolf density such that elk used aspen stands in low wolf density areas but avoided aspen stands in high wolf density areas. Elk also appear to reduce their use of their preferred grassland foraging habitat when wolves are present (Creel et al. 2005), which may be a strategy to reduce predation risk.

However, these studies do not clarify whether displacement of elk or changes in feeding behaviour are responsible for reduced browsing rates. Even if displacement of elk by wolves does not occur or is temporary (Kunkel & Pletscher 2001), predation risk may reduce overall browsing pressure by interrupting feeding or reducing the number or duration of visits made to risky patches. Alternatively, elk may favor the edges of dense aspen or willow stands (White et al. 2003) in risky areas, thereby reducing browse intensity in the center of the patches. To develop a better mechanistic understanding of a trophic cascade that is mediated by indirect effects of wolves on elk it will be important to quantify the relationship between predation risk, willow patch residency time and visitation rate, group size, off-take rates, and winter severity. While increased predation

risk may reduce willow patch residency time (see Abramsky et al. 2002), this may not necessarily result in a reduction in off-take rates if patch visitation rates increase. Severe winters would likely result in higher off-take rates as elk may become increasingly willing visit risky habitats to meet their energy requirements. Predation risk also appears to influence group size (Creel & Winnie 2005), which may affect willow off-take rates if patch residency time changes as a function of group size. Behavioural studies are needed to characterize the complex interplay of these factors.

Conclusions

To demonstrate a trophic cascade is occurring between wolves, elk and willow on the northern range we must demonstrate that elk browse negatively affects willow growth and that wolves affect the intensity of browsing on willow. We have shown that browsing reduces stem growth, but because we do not have historical data on intensity of browsing at our sites we can only address how wolves affect browsing intensity indirectly. We did this by examining whether the presence of wolves was a significant predictor of willow growth after accounting for hydrological, topographic and climatic factors that also influence growth. For both species of willow (*S. boothii* and *S. geyeriana*) the presence of wolves on the landscape was a significant predictor of growth. Given the possible direct and indirect effects that could mediate a trophic cascade, we suggest that there is little evidence to suggest that direct effects could be a significant mechanism at this point in time. This work supports the hypothesis that a trophic cascade between wolves, elk and willow that is mediated by indirect effects of wolves on elk is occurring on the northern range.

While ecologists have largely been preoccupied with studying the direct effects of predation on prey populations (Messier 1991, Boutin 1992, National Research Council 1997), for community conservation the indirect effects of predators may be the most significant (Schmitz 1998, Soulé et al. 2003, Pickett et al. 2005). In this context, understanding these effects is a directive for advancing ecosystem conservation and biodiversity maintenance (Berger et al. 2001, Soulé et al. 2003). Our results suggest that predator restoration has resulted in community-altering effects, and in the longstanding debate over Yellowstone's northern range dynamics, the effects of wolf restoration on communities may prove to be an endorsement of the use of ecological process for conservation (Carroll et al., 2001).

Table 2.1. Aikaike's information criteria scores (AIC), change in AIC score (? $_i$), AIC weights (w_i) and log likelihood values (LL) for the top three of 6 candidate models relating the previous year's ring area (PYRA), the percent of twigs on the stem browsed in the winter preceeding growth (PBRWS), elevation (ELEV), watershed area (WSHED), and average annual snow depth (SNOW), to annual stem ring area of *Salix boothii* and *S. geyeriana* on Yellowstone's northern range.

Model Description	LL	AIC	? $_i$	w_i
Salix boothii				
PYRA, PBRWS	-174.2	358.3	0.00	1.00
PYRA, PBRWS, ELEV	-179.8	371.7	13.37	0.00
PYRA, PBRWS, WSHED	-180.7	373.3	15.02	0.00
Salix geyeriana				
PYRA, PBRWS	-86.99	184.0	0.00	0.49
PYRA, PBRWS, ELEV	-86.24	184.5	0.52	0.38
PYRA, PBRWS, SNOW	-87.37	186.7	2.77	0.12

Table 2.2. Aikaike's information criteria scores (AIC), change in AIC score (? $_i$), AIC weights (w_i) and log likelihood values (LL) for the top candidate models and two reference models relating elevation (ELEV), mean winter North Pacific Index (NPIW), mean annual precipitation (PRECIPA), watershed area (WSHED), the annual Palmer drought severity index (PDSI), a binary variable representing the precense of wolves on the landscape (WOLF), and the northern range elk population size (ELK), to annual stem ring area of *Salix boothii* and *S. geyeriana* on Yellowstone's northern range. Only models with a weight $\geq$ 0.01 are reported for the top models. The reference models include the hightest ranked model with the WOLF variable removed, and the highest ranked model that uses the ELK variable, but not the WOLF variable. Variable abbreviations are described in Methods section.

Model Description	LL	AIC	? $_i$	w_i
Salix boothii				
ELEV, NPIW, PRECIPA, WOLF	-1055.21	2128.41	0.00	0.53
ELEV, NPIW, PRECIPA, WSHED, WOLF	-1054.63	2129.26	0.84	0.35
ELEV, NPIW, PDSI, WOLF	-1057.33	2132.66	4.25	0.06
ELEV, NPIW, PDSI, WSHED, WOLF	-1056.82	2133.63	5.22	0.04
[a] ELEV, NPIW, PRECIPA	-1061.29	2138.58	10.17	0.00
[b] ELEV, PDSI, ELK	-1078.10	2172.20	43.78	0.00
Salix geyeriana				
ELEV, NPIW, WOLF	-705.99	1427.98	0.00	0.81
ELEV, NPIW, STRFLWS, WOLF	-707.24	1432.48	4.50	0.09
ELEV, NPIW, PRECIPS, WOLF	-707.37	1432.74	4.75	0.08
ELEV, NPIW, PRECIPA, WOLF	-708.66	1435.31	7.33	0.02
[a] ELEV, NPIW	-714.25	1442.50	14.52	0.00
[b] ELEV, NPIW, ELK	-724.59	1465.17	37.19	0.00

[a] For reference, the highest ranked model without the WOLF term is shown
[b] For reference, the highest ranked model with the ELK term is shown

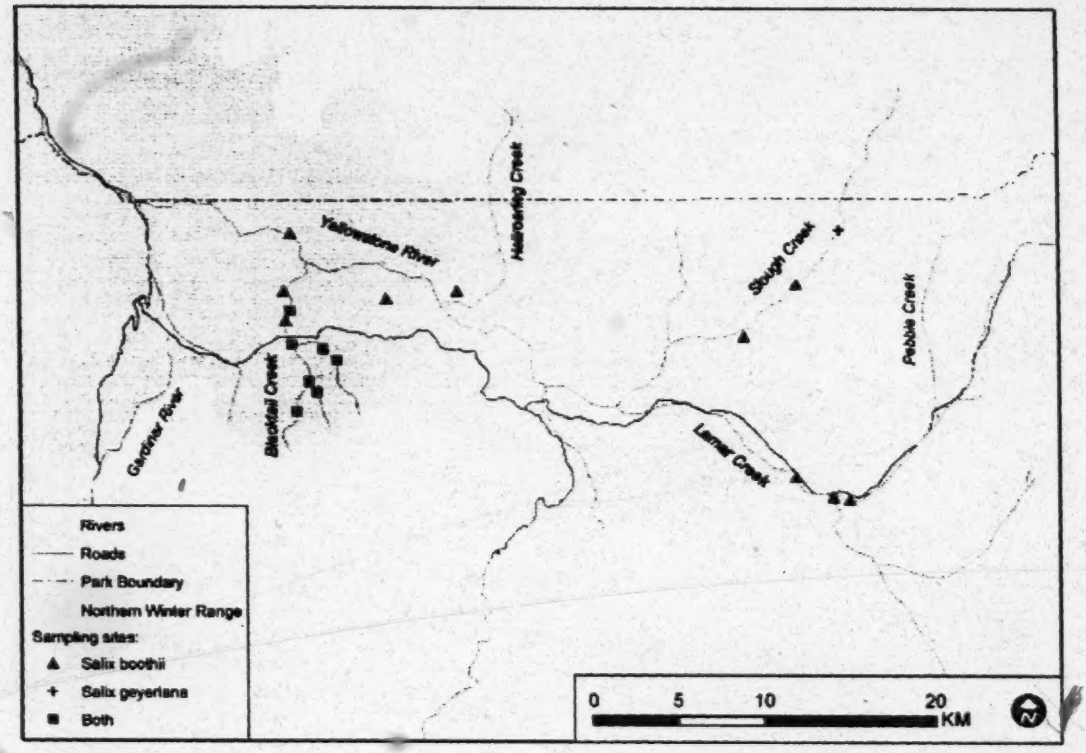

Figure 2.1. Location of willow (*Salix boothii* and *S. geyeriana*) study sites on Yellowstone's northern range.

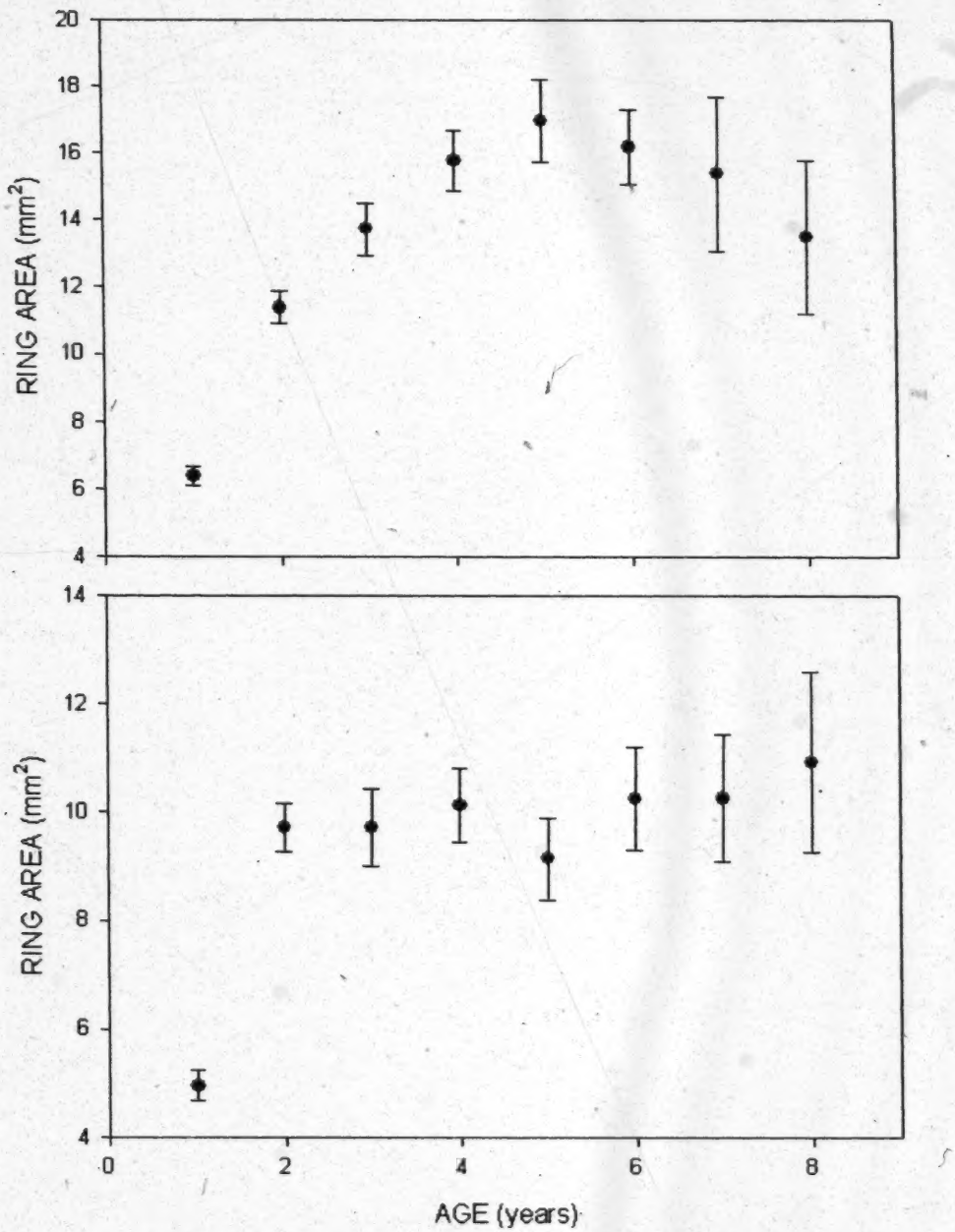

Figure 2.2. Average (± S.E.) annual ring areas (mm^2) for *Salix boothii* (top panel) stems and *S. geyeriana* stems (bottom panel) by stem age (years), from stems collected in 2001 at 17 and 8 sampling sites respectively on Yellowstone's northern range.

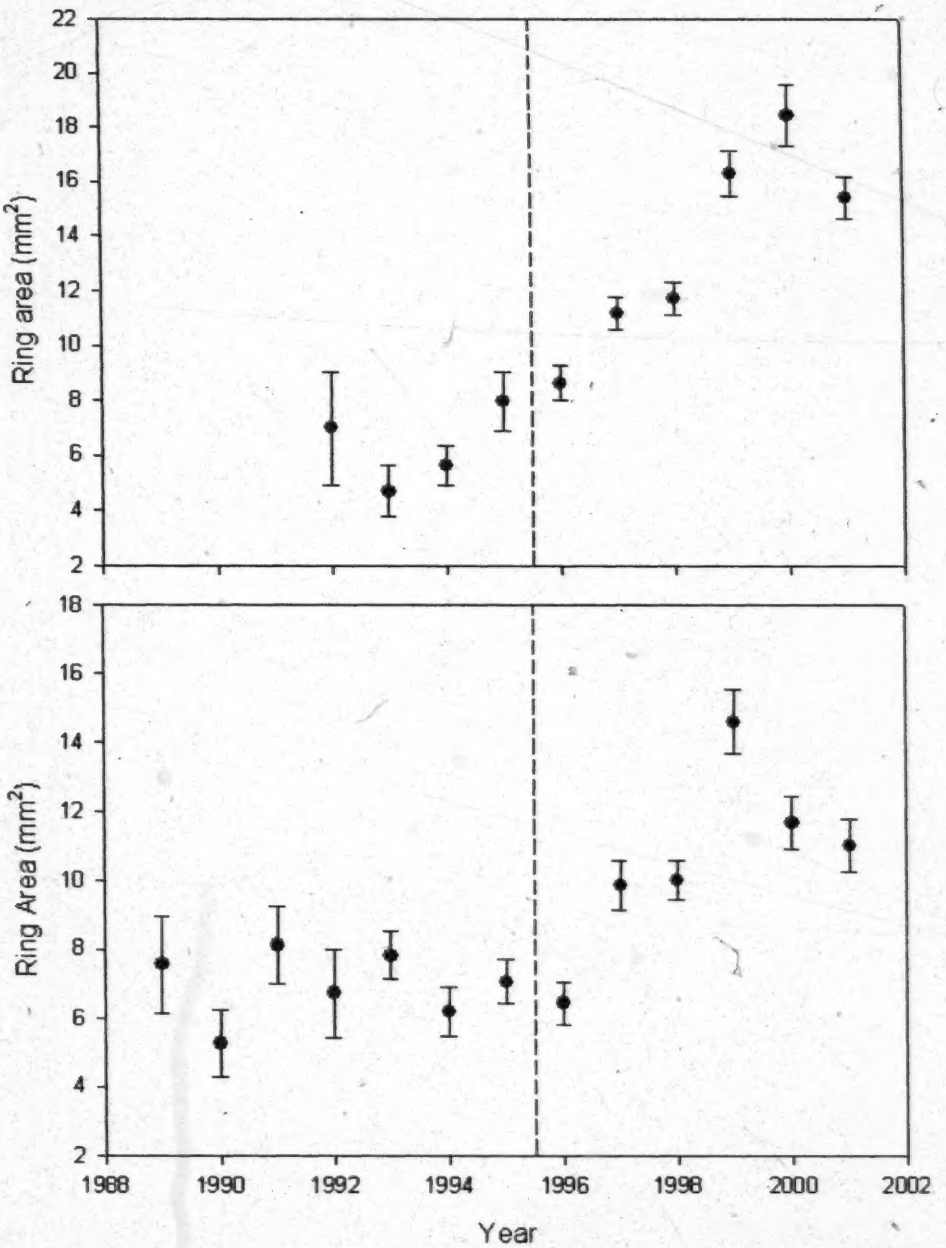

Figure 2.3. Average (± S.E.) annual ring areas (mm^2) for *Salix boothii* (top panel) stems and *S. geyeriana* stems (bottom panel) collected in 2001 at 17 and 8 sampling sites respectively on Yellowstone's northern range. The dashed line represents the first winter in which released wolves were present on the northern range following reintroduction.

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CHAPTER 3

EVIDENCE OF A BEHAVIOURALLY-MEDIATED TROPHIC CASCADE BETWEEN WOLVES, ELK AND WILLOW ON YELLOWSTONE'S NORTHERN RANGE

3.1 INTRODUCTION

Trophic cascades in terrestrial systems occur when changes in predator abundance result in changes in the distribution and abundance of vegetation via the influence of the predator on herbivores (Polis 1999, Schmitz et al. 2000). While trophic interactions between predators and prey are common (Sih et al. 1985), not all trophic interactions cascade (Strong 1992). Trophic cascades have been demonstrated in aquatic (Carpenter & Kitchell 1988, Estes & Duggins 1995) and invertebrate (Schmitz et al. 2000) systems, but may be less common in mammalian terrestrial systems (Strong 1992). Mammalian predator food webs are often complex and highly interconnected, with higher herbivore diversity in the intermediate portions of the food web that buffers the system against the influence of any one predator (Strong 1992, Polis & Strong 1996, Schmitz et al. 2000). Trophic cascades are mediated by direct effects, whereby a reduction in prey numbers or density results in a decreased consumption of vegetation (Strong 1992), and indirect effects, whereby predators alter the behaviour and distribution of herbivores (Abramsky et al. 2002, Ripple & Larson 2000) thereby creating local refugia for vegetation (White et al. 1998, Ripple & Beschta 2004a, Ripple & Beschta 2004b, Hebblewhite et al. 2005).

A trophic cascade may be responsible for increased growth of willow (*Salix* spp.) on Yellowstone National Park's (YNP) northern range (Ripple & Beschta 2003, Ripple & Beschta 2004a, Beyer 2005) following the reintroduction of wolves (*Canis lupus*) in 1995 after an absence of about 70 years (Bangs & Fritz 1996). Historical photographs show

that willow was once abundant and tall on the northern range, but that it has declined by approximately 50-60% since the early 1900's (Chadde & Kay 1991, Soulé et al. 2003). Several factors have been implicated in this decline, including climate and/or hydrology (Houston 1982, Romme et al. 1995, Singer et al. 2000), the loss of beaver (*Castor canadensis*) and beaver ponds (Singer 1996), the severe droughts of the 1930's (Houston 1982, Singer 1996), and high elk (*Cervus elaphus*) densities resulting in high levels of browsing (Chadde and Kay 1991, Wagner et al. 1995, Kay 1998).

While all of these factors are likely to influence willow growth and abundance, increases in willow growth in the last decade that coincide with wolf reintroduction have fueled interest in a potential trophic cascade. In particular, it is hypothesized that indirect effects of wolves on elk have reduced browse rates on willow, thereby facilitating increases in willow growth and abundance in certain areas (Ripple & Beschta 2003, Ripple & Beschta 2004b, Beyer 2005). Although the food web on the northern range is complex (Smith et al. 2003), there are strong interactions between wolves, elk and willow that may facilitate a trophic cascade: elk constitute 90% of the wolf diet (Mech et al 2001, Smith et al. 2004), and elk browse willow heavily in winter (Houston 1982, Singer et al. 1994). There is little evidence to support alternative explanations of the increase in willow growth. Although there is some evidence that direct (lethal) effects of wolves on elk may have reduced the elk herd following reintroduction (White & Garrott 2005), elk density on the northern range still exceeds 8 elk/km^2, a density eight times higher than the maximum density White et al (1998) suggested would result in release of aspen in Banff National Park. Furthermore, the change in elk density since wolf reintroduction is poorly

associated with willow growth in those years, as are abiotic (climatic, topographical and hydrological) factors (Beyer 2005).

This paper examines whether movement patterns of elk in response to predation risk could be responsible for the reported increase in willow growth (Ripple & Beschta 2003, Ripple & Beschta 2004b, Beyer 2005) on Yellowstone's northern range. Previous work has suggested that elk respond to wolves by shifting their habitat selection, leading to reductions in the use of aspen and willow stands (White et al. 2003, Fortin et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005). We build on these studies by evaluating the use of riparian areas by elk while accounting for other environmental conditions that previous work has indicated influences elk movement (Bergman et al. 2005, Creel & Winnie 2005, Fortin et al. 2005) and habitat selection (Boyce et al. 2003, Mao et al. 2005). However, this previous work has not considered how habitat selection or movement patterns may vary throughout the day, even though daily cycles in elk behaviour are pronounced (Ager et al. 2003, Forester 2005). By not considering time of day, it is possible that strong selection for or against environmental conditions may not be detected if the selection reverses at different times of day (e.g. day versus night).

Nor have these studies examined the influence of perceptual cues on movement or distribution, which has been shown to be important for other vertebrates (Lima & Zollner 1996, Zollner & Lima 1999a, Zollner & Lima 1999b). Because wolves have higher kill success when they are able to closely approach prey without detection (Kunkel & Pletscher 2001), we hypothesize elk may select areas that allow an improved ability to detect approaching wolves. We therefore develop a new method ("viewscapes") of

characterizing landscape locations by quantifying the ability of elk to visually detect wolves based on topography, vegetation and line of sight analyses.

We use step selection functions (Fortin et al. 2005) to develop probabilistic models of fine-scale elk movement, and use these models to examine whether the indirect effects of wolves on elk could explain the observed increase in willow growth (Beyer 2005). Secondarily, we examine how step selection patterns vary by time of day, and whether elk movement is influenced by visual cues related to the ability of elk to detect approaching predators.

3.2 METHODS

3.2.1 STUDY AREA AND ANIMALS

This study was conducted on Yellowstone National Park's northern range (Wyoming, USA; 110° 23' W, 44° 55' N), a 1,526 km^2 area characterized by low elevation (1,500–2,000m) grassland (primarily *Festuca idahoensis*) and sagebrush (*Artemisia* spp.) grasslands fringed by coniferous forests (primarily *Psuedotsuga menzeseii, Picea engelmanni* and *Pinus contorta*) and scattered aspen (*Populus tremuloides*) stands (Despain 1990). Mean monthly winter (November-April) temperatures in the winters beginning November 2000, 2001 and 2003 were –5.6°C at Tower Falls (Western Regional Climate Center, Reno, Nevada, USA), and mean daily temperatures during the coldest month (January) were –10.4°C. Mean monthly winter precipitation in these same winters was 11.7cm at Tower Falls, with April being the month of greatest accumulation. With respect to temperature and precipitation these winters were slightly milder than average.

We followed the movements of 18 adult female elk equipped with global positioning system (GPS) telemetry collars (Telonics Inc., Mesa, Arizona, USA) that recorded positions at 5 hour intervals, which results in locations being collected at all hours of the day on a five day cycle. All collars were deployed in February (nine in 2001, seven in 2002, and two in 2003) and remained on the animal for one year or until the animal died. We considered only the locations that occurred within the bounds of the northern range between the months of November to April inclusive.

3.2.2 STATISTICAL ANALYSIS OF ANIMAL MOVEMENT

We used step selection functions (SSF; Fortin et al. 2005) to model elk movement, a statistical approach that is related to resource selection studies having a case-control design (Manly et al. 2002, Boyce et al. 2003). Animal movement can be described as a series of steps and turns, where a step (sometimes also referred to as a leg) is the straight line connecting two consecutive telemetry locations and is described by a distance (step length) and direction, and a turn is the change in direction between consecutive steps (Turchin 1998). The premise of the SSF approach is that landscape characteristics along the step can influence the probability of an animal taking that step. The relative probability of step selection, $w(x)$, is estimated by comparing observed elk steps to a random sample of available steps using conditional logistic regression:

$$\hat{w}(x) = \exp\left(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p\right) \qquad (1)$$

where x_1 to x_p are environmental predictor variables characterized along each step, and β_1 to β_p are coefficients associated with each of those variables estimated by conditional logistic regression. Although SSF is based on characterizing environmental variables

along straight lines, it does not imply that elk would actually travel along these lines, only that the probability of step selection is related to the characteristics of the environment between the start and end points of a step (Fortin et al. 2005).

Based on the daily cycle in the distribution of elk step lengths (Figure 2.1) four time periods were defined that coincided with the peaks and troughs of activity: dawn (steps beginning between 4am – 7am inclusive), day (9am - 12pm), dusk (1pm – 4pm) and night (9pm – 12pm). Comparisons of the step selection functions from each of these time periods were made to determine how time of day influenced movement. Because locations were collected at a 5-hour interval and the time of day periods spanned four hours, the minimum time interval between consecutive locations within each of these four datasets was 21 hours. This resampling of the data was designed to minimize autocorrelation in the datasets.

Steps made by one individual cannot be considered independent from one another. Lack of independence does not influence the beta coefficients estimated by the logistic regression model, but does bias their standard errors (Neilson et al. 2002). We therefore used a robust sandwich estimate of the covariance matrix (Lin & Wei 1989, Wei et al. 1989, Fortin et al. 2005) to calculate robust standard errors. This is achieved by clustering on each animal. We also used autocorrelation and partial autocorrelation plots of model residuals for each animal in each winter to evaluate whether autocorrelation was inherent in the data.

When elk form herds, locations from two or more elk in the same herd cannot be considered independent (Millspaugh et al. 1998). We therefore quantified the level of association between the elk we monitored by counting the number of concurrent locations

that occurred within 100m of each other. Animals within 100m of each other were assumed to be in the same herd.

Model development followed the guidelines in Hosmer & Lemeshow (1989, 1999). Although the significance testing approach to model building has limitations (Anderson et al. 2000) and the information theoretic approach to model development is often considered superior (Burnham & Anderson 1998), Aikake's Information Criteria (AIC) is not robust to autocorrelated data as the calculation of the log likelihood does not take into account the lack of independence in the dataset. Also, in use versus availability designs where the number of available samples is large, AIC is biased towards more complex models. Because our dataset consisted of locations sampled frequently, we expected to find autocorrelation in the residuals of our models. We therefore used the modeling framework developed by Fortin et al. (2005; Appendix I), which is designed to accommodate autocorrelated data.

Predictor variables were selected for consideration when previous research had demonstrated their influence on elk movement and habitat selection, or, in the case of the viewscape metric, that we hypothesized were important. Predictor variables were screened for multi-collinearity by calculating Pearson correlation coefficients between pairs of variables; we assumed correlations >0.6 indicated collinearity. If a variable was collinear with one other variable, we selected the variable we considered to have the greatest biological interpretability. We eliminated a variable if it was collinear with multiple other variables that were not themselves correlated. If there was existing evidence or we suspected that the response to a variable was not linear, we compared models containing linear, square root, squared, or quadratic ($x + x^2$) forms of the variable

and selected the form that resulted in the largest increase in the $?^2$ statistic of the robust Wald test for the hypothesis that the variable had no effect (Fortin et al. 2005). If the coefficient ± the robust SE crossed zero, the variable was eliminated from the model. After all variables had been evaluated in this way, each of the rejected variables was entered back into the model to ensure that no significant variables were omitted. All statistical analyses were performed using the software R version 2.0 (R Development Core Team 2004).

Each observed elk step was compared to 25 random steps that were created by drawing from step length and turn angle distributions based on the observed movement paths of all the elk monitored. Separate step length and turn angle distributions were created for each time of day period (dawn, dusk, day, and night) and Kolmogorov-Smirnov tests were used to test for significant differences between them. Distributions that were not significantly different were merged. Sampled steps were created by drawing from the distributions corresponding to the time of day of the observed elk step. Each step was characterized by creating summary statistics of the spatial predictor variables along each step (see below). Responses of elk to any one variable can be depicted by holding all other environmental conditions constant at their median values and plotting the relative probability of step selection (standardized by dividing by the maximum), $w(x)$, over the range of values over which elk encounter that variable.

Characterization of steps from landscape variables

Many factors can influence elk movement. We selected spatial variables that have previously been demonstrated to be important predictors of elk habitat selection and

movement, or variables we hypothesized would influence elk movement. Random and observed steps were characterized based on the minimum distance along the step to a road (km; DSTRD). A USGS digital elevation model (30m resolution) was used to calculate slope (degrees) across the northern range. The mean slope encountered (degrees; SLP) was calculated for each step, and a dummy variable (SSLOPE) was used to account for steps that crossed slopes steeper than 63 degrees, which we considered to be barriers to elk movement (Fortin et al. 2005). We did not consider elevation *per se* as a predictor variable for two reasons. First, elevation is a proxy for other more mechanistic variables like snow water equivalent or forage biomass, which we choose to represent in our models directly. Second, elevation is typically collinear with several other variables that are not themselves collinear (e.g. slope, snow water equivalent, forage biomass) so could potentially confound interpretation of the influence of these other variables.

A habitat map based on the classification of a Landsat 5 TM satellite image (see Forester 2005 for details) was used to determine the mean distance to forest-meadow edge along each step (m; DSTED). We grouped aspen, mixed deciduous/conifer forest, unburned forest, and forest that had burned in the 1988 fires for this calculation as all provide concealment for elk and are hard edges (Bergman et al. 2005). A dummy variable (OPEN) was used to differentiate steps that ended in open habitat (1) from those that ended in forested habitats (0).

Herbaceous forage biomass was estimated based on 60-m vegetation sampling transects positioned at 83 random locations, and stratified by six cover types derived from the habitat classification (see Forester 2005 for details). Each transect was sampled four times from mid June to late August in 2003. Forage biomass was estimated by measuring

the height of a plastic 0.25-m^2 disk placed on the vegetation at six plots along each transect. Disk height was calibrated with dry biomass (samples dried to constant mass at 40° C for 48 hours and then weighed) within 5 functional groups (forb, grass, sedge, rush, woody vegetation) based on 214 plots clipped to ground level (see Forester 2005, pp.75-81, for a complete description of methods). A predictive model of peak biomass at each transect was developed using two predictor variables: 1) the normalized vegetation difference index (NDVI) derived from the red and near infra-red bands of an August Landsat 5 TM image, and 2) the compound topographic index (CTI; Gessler et al. 1995), which represents relative soil wetness (see Forester 2005). The mean peak forage biomass encountered along the step (g/m^2; BIOM) was used in our analyses.

The minimum distance along the step to riparian areas (km; DR) was calculated based on permanent streams and rivers delineated in the National Wetland Inventory (USGS). This data includes all streams on which we found willow, but omits the very small ephemeral streams that, based on our surveys of willow on the northern range, do not support willow communities. Also, the ephemeral streams are unlikely to be a significant barrier to elk movement because of their small size.

Snow water equivalent (SWE) maps for the study area were generated on a daily basis for each winter (1 November to 30 April the following year) using a model by Cougenhour (1994). These daily maps were averaged to create one mean SWE map for each half of every month (days 1 to 15, and days 16 to the end of the month). The mean snow water equivalent (mm) encountered along a step was determined from the SWE map corresponding to the date of that step.

An index of wolf density was created for each winter based on VHF telemetry data supplied by the Yellowstone Wolf Project (D.W. Smith, YNP). Wolves in each pack were relocated using aerial telemetry on an approximately weekly basis from November to April, with periods of more frequent (approximately daily) relocations from mid-November to mid-December and in March. Data were filtered to eliminate records from more than one individual in the same group on the same day. Bivariate normal kernels density estimates with a 3km fixed bandwidth were generated for each winter (Fortin et al. 2005). This wolf index (WOLF) represents areas where wolves are more likely to be found on the northern range.

Predator detection

We devised a metric ("viewscapes") to quantify the ability of elk to detect predators. Viewscapes estimate the proportion of area in a given radius around a location that can be visually observed by an animal positioned there, and take into account the height of the animal and the line of sight obstructions caused by topography and trees (Figure 2.2). The viewscape calculation is performed at regular intervals (e.g. 30m) across the landscape to create a continuous surface of this metric.

Viewscapes were based on a viewshed algorithm (Wang et al. 2000) calculated in a GIS (ArcGIS; Environmental Systems Research Institute, 2004) using grid-based (raster) data representations. The elevation of the observer was determined by adding the height of the eye above the ground (2m for elk) to the elevation above mean sea level of the observer, which was queried from a standard USGS digital elevation model (DEM). We quantified the area in a 100m radius that could be visually observed by an elk. We

assume that the perceptual range of elk in forest is limited to their immediate vicinity and the metric is therefore 0. When elk were in open habitat, the line of sight calculations were based on a DEM that was adjusted to include the height of vegetation: 10m was added to the DEM in all forested areas. Locations within the 100m radius that were forested, or that were obstructed from view by topography or vegetation were counted as not visible. Non-forested locations that could be directly observed by the elk were considered visible. We summarized the mean viewscape metric (VSCAPE) value along each step. The characterization of steps was made using custom programs written for ArcGIS 9.0 (Environmental Systems Research Institute 2004).

Use of willow patches

A map of willow on the northern range was created based on extensive aerial and ground surveys conducted during the summers of 2001 and 2002. Potential willow sites identified from the aerial surveys were subsequently visited on foot to verify the presence of willow, identify the species present, and record the location with a GPS unit. These coordinates, along with sketches from the aerial survey, were then converted to a digital map using a GIS and 1m resolution black and white orthophotographs as reference. To determine if use of willow occurred more frequently at certain times of day, we identified all elk locations falling within 100m of the mapped willow patches and used a binomial test to compare frequency of use between day and night.

3.3 RESULTS

The median fix rate for the 18 GPS collars was 87.6% (range: 56.1% to 95.7%), resulting in 1458, 1451, 1469, and 1527 observed steps in the dawn, day, dusk and night time of day periods respectively. Elk locations were spread across the northern range, but were rare in the higher elevation portions of certain drainages including Slough Creek, Soda Butte Creek, Cache Creek and the upper Lamar valley. Associations between elk occurred for short periods of time (mean rate: 2.96 relocations over 2.00 consecutive days) for 11 pairs of elk (of a total of 115 possible pairings). The greatest association detected was 8 relocations over 3 days between animals #2 and #8. Since no two elk were associated for more than 3% of their time within a winter, we assumed that the animals were independent in this analysis. The mean distance between concurrent elk locations for the 18 elk we monitored was 16.6 km.

The distribution of step lengths was not different between dawn and dusk (two sample Kolmogorov-Smirnov test, $D = 0.102$, $p = 0.920$), or night and day (two sample Kolmogorov-Smirnov test, $D = 0.102$, $p = 0.920$), but was different between night/day and dawn/dusk (two sample Kolmogorov-Smirnov test, $D = 0.322$, $p = 0.00440$). We therefore merged the step length distributions from day and night (Figure 2.3a), and from dawn and dusk (Figure 2.3b). Turning angle distributions were not different between any of the time periods (two sample Kolmogorov-Smirnov test, $D = 0.25$, $p = 0.211$ for all comparisons), therefore all four turning angle distributions were merged (Figure 2.3c).

Elk movements were influenced by multiple environmental conditions in each time of day period (Table 2.1). The SSF models provide probabilistic movement rules for elk in each time of day period, where the choice of a given step is contingent upon the set

of available steps at each location (Fortin et al. 2005). Elk avoided taking steps that passed within 0.2km of riparian areas (Figure 2.4), and steps that crossed very steep slopes or high amounts of snow, at all times of day (Table 2.1). Elk also selected steps with higher mean forage biomass at all times of day except dusk (Table 2.1). Selection for minimum distance to roads varied by time of day: during the day elk avoided being close to roads, but switched to selecting steps closer to roads at dusk and night (Figure 2.5). During the day the mean distance to roads was 690m (± 330m SD), whereas at night it was 570m (SD = 340m). During the dawn and day elk selected for intermediate slopes, averaging 29.3° (SD = 13.9°) and 32.0° (SD = 14.1°) respectively. We found no evidence that slope influenced elk movement during dusk, although the mean slope of steps taken by elk at dusk was 32.5° (SD = 13.3°), similar to other times of day. Elk were more likely to select steps in slightly flatter areas at night (mean slope 28.4°, SD = 15.0°). Although elk avoided taking steps crossing high amounts of snow at all times of day, they were also less likely to take steps crossing areas of very little snow at dawn and during they day. During dusk and night, elk were more likely to select steps crossing areas with low amounts of snow.

Elk were more likely to take steps that ended in open habitats during the day and night than would be expected at random (Table 2.1). In the day, 63.5% of elk locations occurred in open habitats, but this increased to 79.1% at night. Distance to edge was not a significant predictor of step selection in the day and night models. However, there was an interaction between the OPEN and DSTED variables in the dawn and dusk models (Table 2.1) that implies that elk respond differently to edge in open and forested habitats. At dawn, steps in open habitats are more likely to end closer to the forest edge, and steps in

forested habitats are more likely to end further from the forest edge (Figure 2.6a). This is consistent with elk transitioning from open to forested habitats at dawn. The selection patterns are reversed at dusk (Figure 2.6b), which is consistent with elk transitioning back into open habitats at dusk.

During daylight hours (the dawn, day and dusk models) elk were more likely to take steps that allowed greater ability to detect predators (Table 2.1), as indicated by the viewscape metric (VSCAPE). This metric was not a significant predictor of step selection at night (Table 2.1). The wolf index was a significant positive predictor of elk step selection in the dawn and day models, but had no significant effect in the dusk and night models (Table 2.1). No significant interactions with the wolf index were found in any of the models.

Although elk generally avoided riparian areas, 131 locations fell within 100m of the mapped willow areas. These locations were not distributed equally throughout the day (Figure 2.7). Elk were more likely to use willow areas during the night (9pm to 9am) than during the day (binomial test, $?^2 = 32.3$, df = 1, p-value < 0.001).

No evidence of autocorrelation was found in the residuals of any of the models. Autocorrelation and partial autocorrelation plots for each animal in each winter for 1-40 lags showed no evidence of correlation.

3.4 DISCUSSION

Our results are consistent with the hypothesis that the increased growth of willow on the northern range is mediated by the behavioural response of elk to the risk of predation by wolves (Laundré et al 2001, Ripple et al. 2001, White et al. 2003, Ripple &

Beschta 2004a, Hebblewhite et al. 2005). Elk consistently avoided being close to riparian areas at all times of day, which may be a strategy to avoid areas of high vulnerability to predation as previous research suggests that ungulates are more susceptible to predation in riparian areas (Kunkel & Pletscher 2001, Bergman et al. 2005, Ripple & Beschta 2004). Bergman et al. (2005) found that elk in west central Yellowstone were most vulnerable to wolf predation along hard edges (meadow/forest edges and riparian areas) and suggest that this is caused by a decrease in speed, maneuverability and escape routes when hard edges are encountered. Wolves are more successful at making kills in ravines, close to water, and on ice (Kunkel & Pletscher 2000, Kunkel & Pletscher 2001). Riparian vegetation and terrain might also allow predators to closely approach prey without detection, giving wolves the element of surprise and increasing the probability of killing prey (Kunkel & Pletscher 2001). Furthermore, encounter rates with wolves may be higher in riparian areas because the risk associated with killing prey may result in strong wolf selection for habitat types or environmental conditions in which the probability of a kill without injury is higher, even if this means hunting in areas where prey occur at lower densities. Smith et al. (2004) report that 6 wolves have been killed by prey since reintroduction (5 by elk and 1 by a moose), and Bergman et al. (2005) report that wolves preferred to travel along hard edges and argue this is because they are selecting routes through habitats in which prey are most vulnerable. Thus, riparian areas are risky to elk not only because of increased vulnerability to wolves, but also because the probability of encountering wolves may be higher if wolves favor them as travel routes.

We found no evidence that a trophic cascade in Yellowstone was ultimately mediated by human disturbance. White et al. (1998, 2003) and Hebblewhite et al. (2005) suggested

that a trophic cascade between wolves, elk and aspen/willow in Banff National Park was ultimately mediated by human disturbance: wolves avoided areas frequented by humans that created local refugia for elk, which were occupied at high densities. Aspen and willow within these refugia were heavily browsed compared to areas of high wolf density away from human disturbance. We found that elk did avoid close proximity to roads during the day, which corresponds to the time of highest human use, but elk selected steps close to roads at night. We also show that use of willow is highest during the night (when elk are closest to roads), thus human disturbance cannot ultimately be responsible for a trophic cascade on the northern range.

Daily cycles in the effects of environmental conditions on elk movement

Elk movement is influenced by many biotic and abiotic components of the environment (Kie 1999, Fortin et al. 2005), and the response of elk to many of these factors varies by time of day. The movement patterns observed appear to reflect the tradeoff between regulating energy intake and expenditure (selecting good foraging sites, seeking shelter) and mediated the risk of predation by avoiding high-risk habitats, while also avoiding obstacles to movement (steep slopes, deep snow) and human activity near roads during the day.

We found that time of day had a strong influence on elk movement and habitat selection, consistent with other studies that have noted a circadian cycle in elk behaviour with crepuscular hours used as transition periods between foraging and secure resting habitats (Ager et al. 2003, Green & Bear 1990). While the response of elk to some environmental conditions was consistent throughout the day (forage biomass, distance to

riparian habitat, avoidance of steep slopes), the response to other conditions varied (snow water equivalent) and in some cases even reversed (distance to edge). On the winter range elk clearly favored open habitats at night, and a mix of open and forested habitats during the day. The patterns of selection of distance to edge we observed at dawn and dusk were consistent with elk transitioning from forested to open habitat at dusk and open to forested habitat at dawn. Although elk may mediate predation risk by adjusting their position relative to forest cover (Creel & Winnie 2005, Creel et al. 2005), we found no clear relationship between distance to cover and wolf risk.

Several of the environmental variables we examined co-vary, and this must be considered when interpreting the results of our models. For instance, the dawn model appears to indicate that elk were less likely to select steps in areas of low amounts of snow. This may seem counterintuitive as snow impedes movement (Sweeney & Sweeney 1984), reduces access to forage, and may increase susceptibility to predation (Kunkel et al. 2004). However, this pattern must be interpreted in the context of elk shifting between use of open and forested habitats. At night most elk locations (~80%) were in open areas, which tend to have less snow than forested areas because they are generally at lower elevation and wind removes snow from open areas. During the day elk use of open areas decreases (~60% of locations). The apparent avoidance of low snow areas may be caused by this transition of use from mainly open areas at night to a mix of forest and open areas during the day, given that forested areas tend to have more snow. Similarly, elk appear to select for flat areas at night. In fact this relationship is likely to arise because elk select open areas at night. Slopes in open areas can be shallow because many open areas occur in the valley bottoms whereas the steeper sides of the valley are forested (e.g. Lamar and

Slough drainages). Care must therefore be exercised when interpreting the models to distinguish between selection for factors that drive movement patterns versus factors that are merely proximate.

We found that during daylight hours elk selected steps that facilitate predator detection, as quantified by the viewscape metric. This could be an important factor discouraging use of willow areas by elk in the smaller drainages (e.g. Blacktail Creek, Crystal Creek) that occur in gullies where perceptual range is limited (Ripple & Beschta 2003, Ripple & Beschta 2004a, Ripple & Beschta 2004b). It is likely that elk avoid riparian areas for a multitude of reasons, of which limited perceptual range is just one. The taller vegetation adjacent to streams could allow wolves to approach elk without detection, thereby increasing predation risk to elk. Steep slopes, debris on the floodplain, ice along the riverbank and the river itself could act to limit escape routes. Ridge tops might allow wolves vantage points from which to scan for prey. Deeper snow accumulations in gullies could impede movement. And the use of hard edges as wolf travel routes could result in higher rates of elk encountering wolves. It is difficult to identify which, if any, of these explanations if of greater importance than the rest.

Responses to wolves

We found some evidence that wolves and elk were spatially associated: our wolf index, which characterized wolf use within an entire winter, was positively associated with the relative probability of elk step selection at dawn and during the day. Other studies in Yellowstone also report a positive correlation in space use of elk and wolves (Bergman et al. 2005, Fortin et al. 2005, Mao et al. 2005). The inability of elk to spatially

segregate themselves from wolves within a winter or seasonal time frame may arise because once elk are on their northern winter range they have limited ability to avoid wolves, which can rapidly modify space use in response to local changes in prey abundance (Dale et al. 1994, Kunkel et al. 2004). Any attempt by elk to leave the northern range after the onset of winter would result in exposure to more adverse conditions (higher elevations, more snow, less forage biomass, etc) because the northern range is a valley surrounded by higher elevation mountains and plateaus.

The behavioural response of elk to wolves can occur on a gradient of time scales: 1) at a fine time scale (immediate action) elk can be vigilant in an attempt to detect approaching predators and can flee once a pursuit has begun; 2) at a time scale of hours or days elk may mediate predation risk by adjusting their position relative to a suite of environmental covariates that may affect probability of encountering, and susceptibility to, predators; and 3) on longer time frames elk may move to new areas in the landscape or even emigrate to avoid areas of high wolf use. Studies of resource use that sample predator and prey locations on a time scale of hours to weeks are primarily concerned with the second level of behavioural response. Given that the elk are resident on the northern range over winter, and that elk constitute 90% of the wolf diet (Smith et al 2004), it is not surprising that wolves are spatially associated with elk over the seasonal time frame that we summarized wolf use.

The fact that we did not find a positive association between wolves and elk in the dusk and night models may reflect sampling bias in the wolf telemetry data, which was collected using aerial telemetry of VHF collars. There was a strong morning bias to these locations: 74% of the wolf data was collected between 7am and 12pm, and no locations

were collected during the night (after 6pm). There may also be a fair-weather bias in the data, as flights could not occur during adverse weather conditions. It is not clear how these biases affect our analysis. However, Theuerkauf et al. (2003) report that wolves were most active during crepuscular hours, were more active at night than during the day, and were least active from 12pm to 4pm. Also, wolves killed most prey around sunrise with a peak 2.3 hours (± 0.5 hrs) before sunrise and rarely killed in the middle of the day (Theuerkauf et al. 2003). If a similar activity pattern exists among the wolves in Yellowstone, then a mid-morning bias to wolf telemetry locations could be a significant obstacle to quantifying the response of elk to wolves: the most pronounced response to wolves may occur during the times when wolf locations are not sampled. This may explain why we found no evidence that elk responses to environmental conditions changed as a function of intensity of wolf use.

We found no evidence that avoidance of riparian areas increased in response to increases in the wolf index. Sih (1980) suggests that behavioural responses of foragers to the risk of predation can either be constant, or that alterations in behaviour are greater in response to greater risks of predation. Our results suggest that the avoidance of riparian areas is constant. Wolves are a far ranging, quick moving species that can alter space use rapidly (Kunkel et al. 2004). Elk may not therefore be able to predict wolf density or occurrence on the time scale of the steps we measured (5 hour interval locations). If elk cannot reliably predict wolf occurrence and therefore avoid direct contact with wolves, the next best anti-predator strategy is for elk to consistently avoid locations where they are more susceptible to wolf predation and where there is increased ability to detect approaching wolves (Sih 1997). Our results are consistent with this strategy.

Table 3.1. Coefficients and robust standard errors for the final step selection function (SSF) models from each of the four time-of-day periods, based on the analysis of GPS telemetry data for 18 elk resident on Yellowstone's northern range in the three winters (2000-2003). The probability of step selection is modeled as a function of a suite of environmental conditions that influence elk movement including distance to roads (DSTRD), distance to riparian (DR), open habitat (OPEN), distance to edge (DSTED), snow water equivalent (SWE), slope (SLP), the presence of a very steep slope (SSLOPE), forage biomass (BM), a wolf index (WOLF), and the viewscape metric (VSCAPE). See text for details.

	DAWN		DAY		DUSK		NIGHT	
	ß	SE	ß	SE	ß	SE	ß	SE
DSTRD	3.230	0.437**	3.613	0.601**	0.890	0.294**	-0.783	0.170**
$DSTRD^2$	--	--	-1.258	0.270**	-1.516	0.210**	--	--
DR	2.271	0.363**	1.905	0.506**	2.120	0.544**	2.462	0.497**
DR^2	--	--	-1.039	0.435*	-2.052	0.579**	-1.024	0.456*
OPEN	-0.185	0.082*	0.115	0.072	0.461	0.103**	0.317	0.060**
DSTED	0.804	0.483	--	--	-1.414	0.753	--	--
OPEN*DSTED	-2.698	0.671**	--	--	2.346	0.790**	--	--
SWE	1.304	0.245**	0.690	0.181**	-1.406	0.094**	-0.154	0.073*
SWE^2	-0.084	0.020**	-0.049	0.014**	--	--	--	--
SLP	0.920	0.201**	0.589	0.165**	--	--	-0.084	0.037*
SLP^2	-0.087	0.020**	-0.051	0.016**	--	--	--	--
SSLOPE	-1.316	0.163**	-0.859	0.150**	-0.884	0.119**	-0.793	0.249**
BM	0.093	0.025**	0.079	0.028*	--	--	0.054	0.019**
WOLF	0.726	0.261**	0.989	0.128**	--	--	--	--
VSCAPE	0.445	0.224*	0.352	0.179*	0.442	0.215*	--	--

Notes: (*) denotes coefficients significant at the p=0.05 level, (**) denotes coefficients significant at the p=0.01 level.

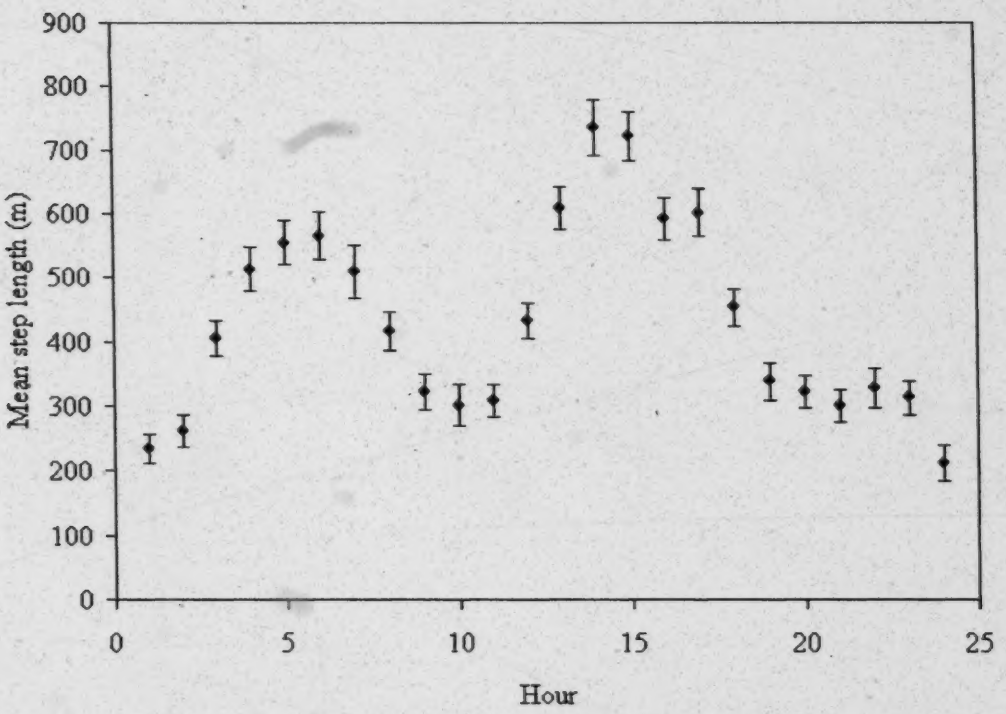


Figure 3.1. Mean (± S.E.) step length (m) by time of day (hour) for 18 elk (*Cervus elaphus*) on Yellowstone's northern range equipped with GPS telemetry collars that sampled locations on a 5-hour interval during three winters. The time represents the start time of the step.

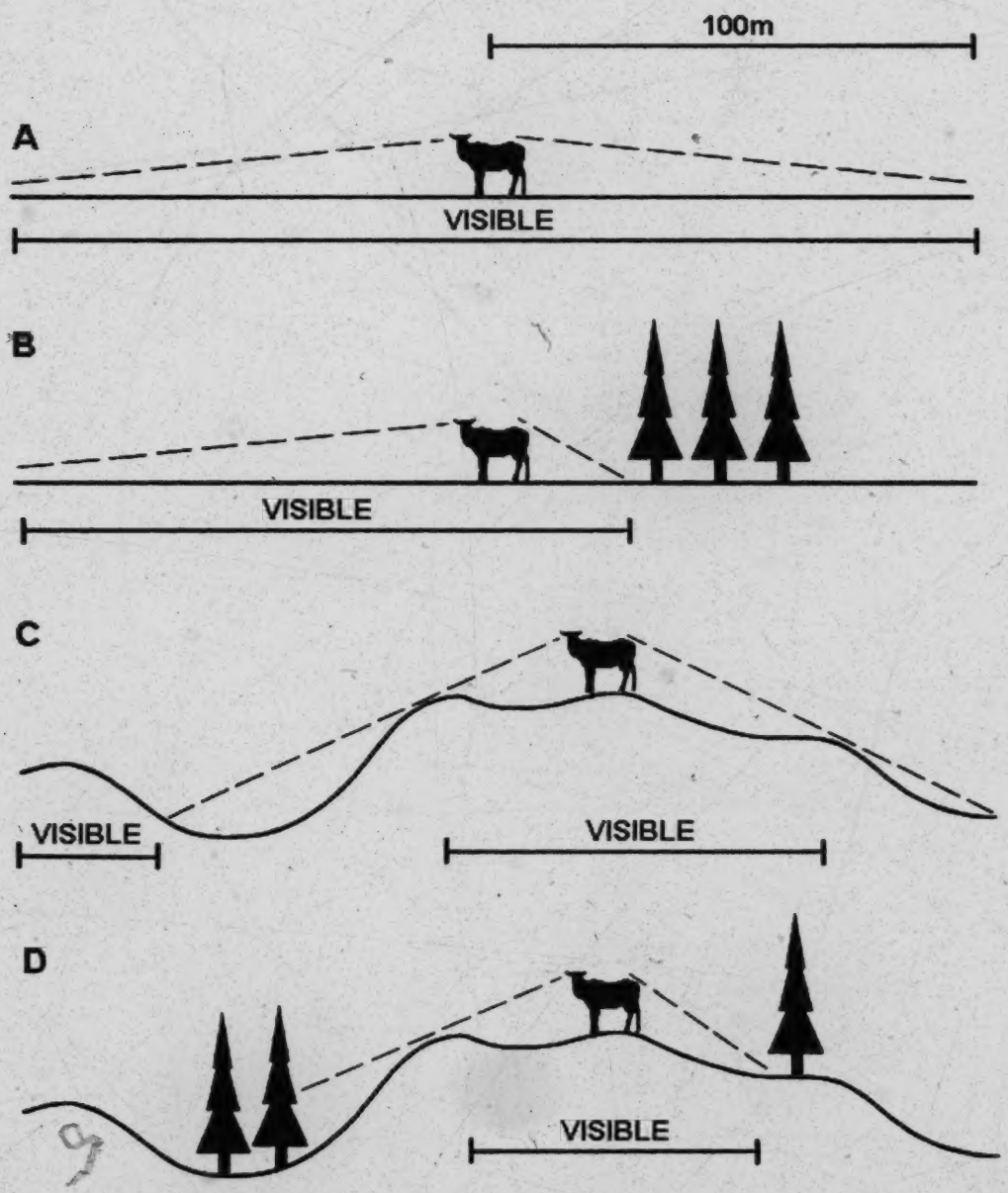
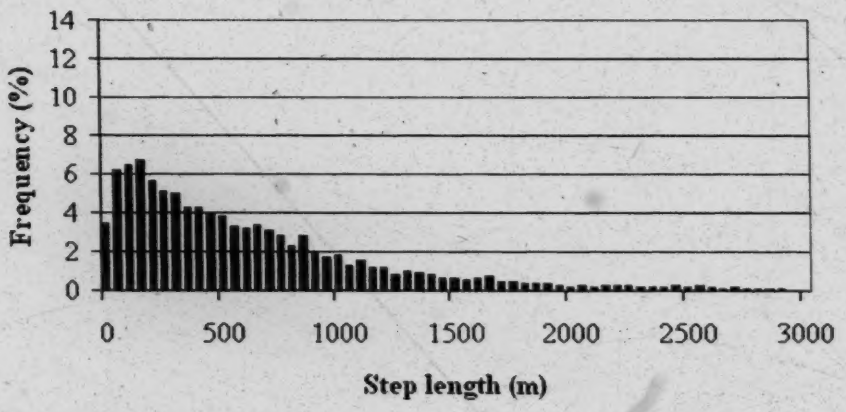
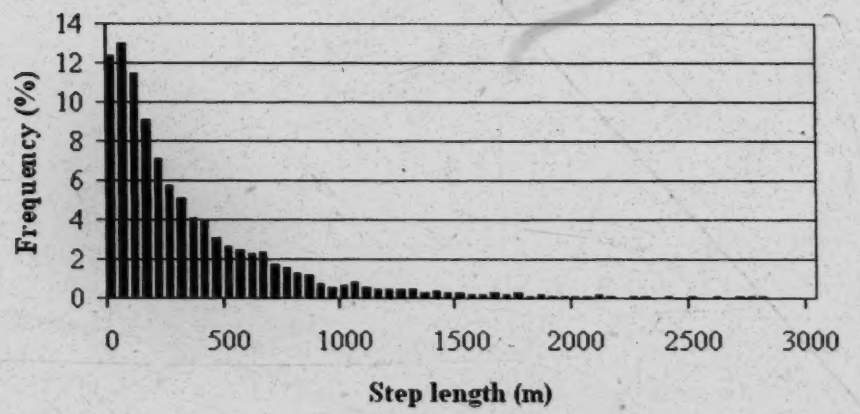


Figure 3.2. The viewscape metric estimates the proportion of area in a given radius around a location that could be visually observed by an animal positioned there. It takes into account the height of the animal and the line of sight obstructions caused by topography and trees. With no obstructions (A), the metric has a value of 1.0. As trees and topography obstruct more of the landscape (B, C, D) the metric approaches 0.

(a)



(b)



(c)

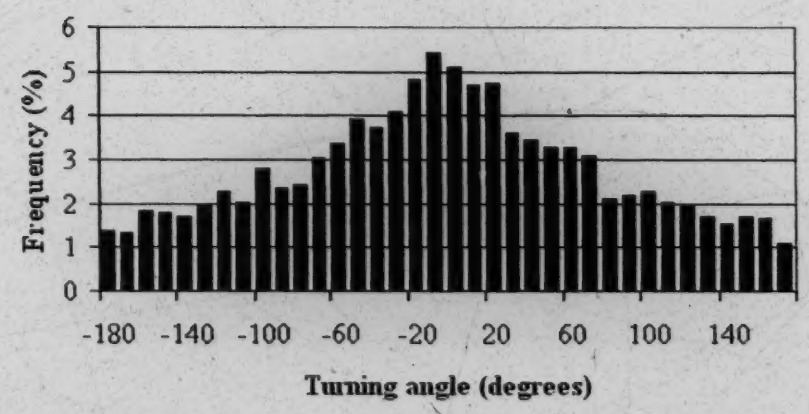


Figure 3.3. Distribution of step lengths (m) during day and night (a), distribution of step lengths (m) during dawn and dusk (b), and distribution of turning angles (degrees) across all times of day (c) based on movement paths of 18 elk monitored with GPS telemetry collars during three winters on Yellowstone's northern range.

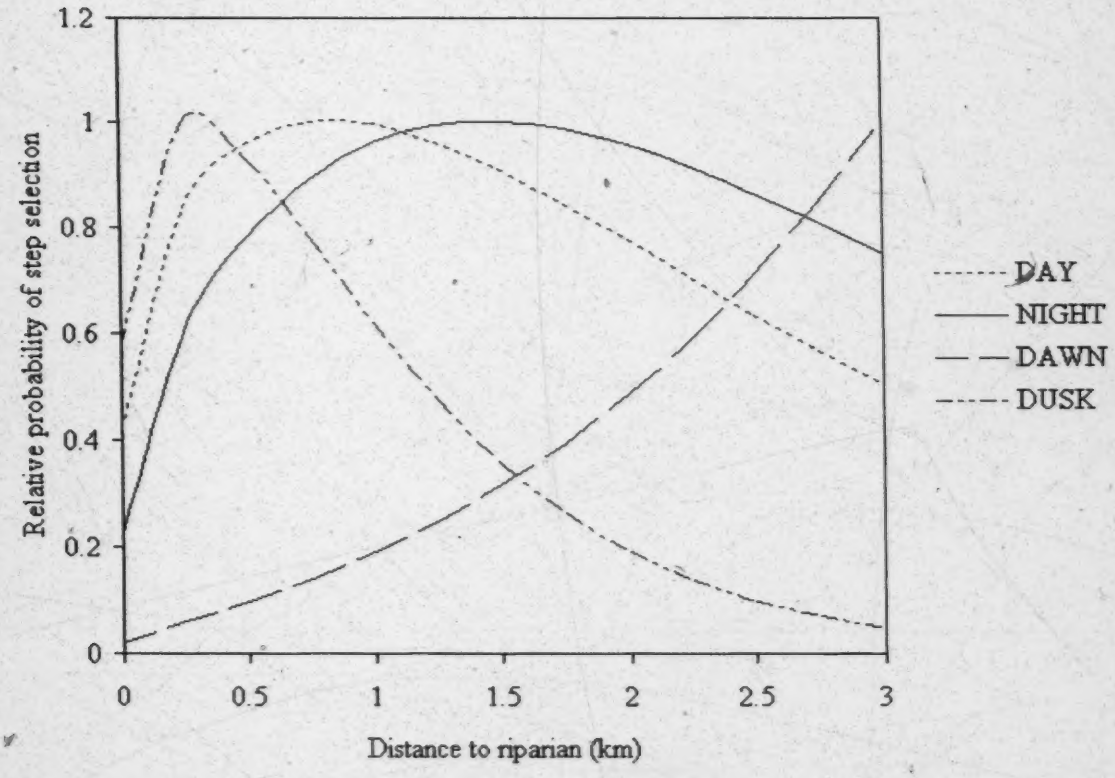


Figure 3.4. Relative probability of a step being selected by an elk at four times of day on its winter range given the minimum distance to riparian habitat along the step, as calculated from the step selection function (SSF) models provided in Table 2.1. Elk consistently avoid steps passing within 100m of riparian areas.

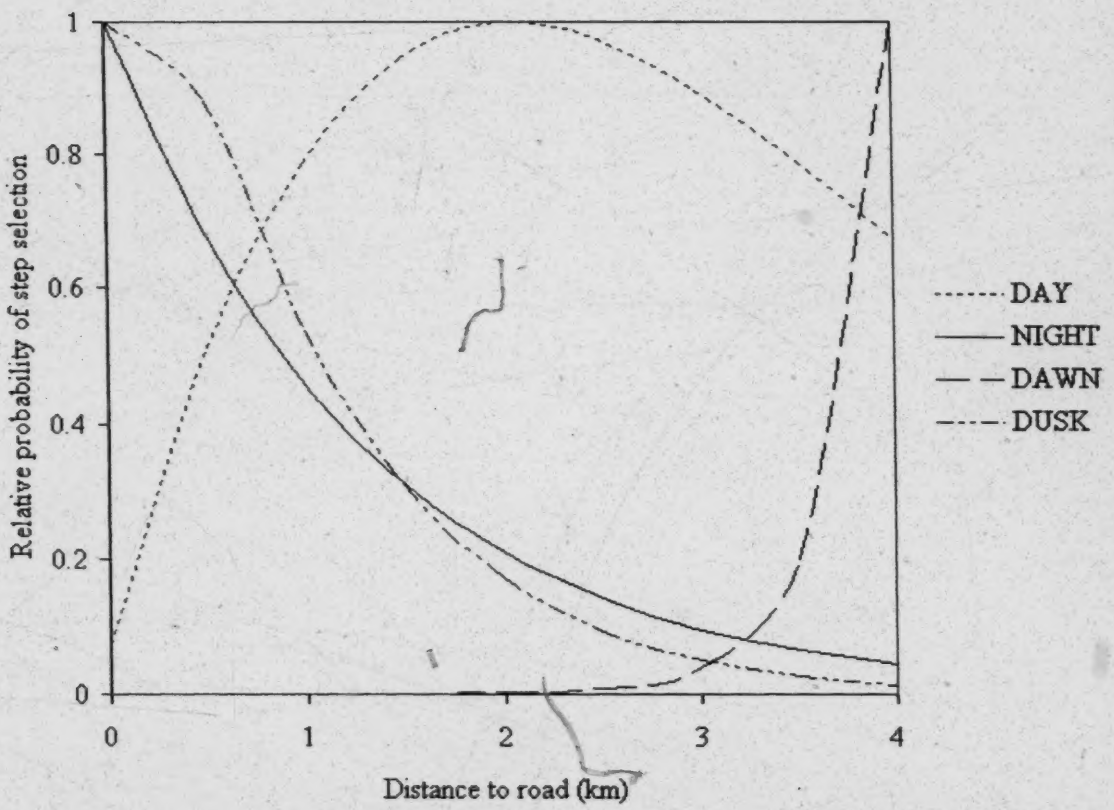
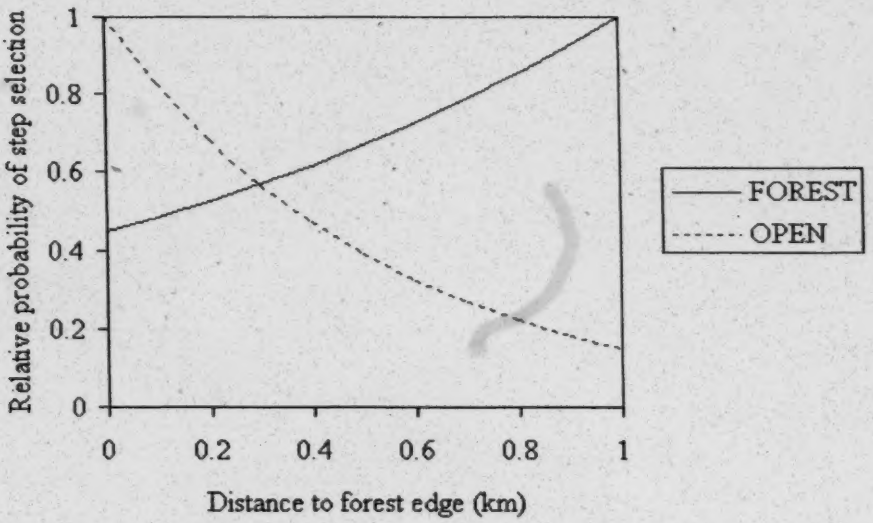


Figure 3.5. Relative probability of a step being selected by an elk at four times of day on its winter range given the minimum distance to roads along the step, as calculated from the step selection function (SSF) models provided in Table 2.1. Elk avoid being close to roads during the day when human activity is highest, but move closer to roads at dusk and during the night.

(a)



(b)

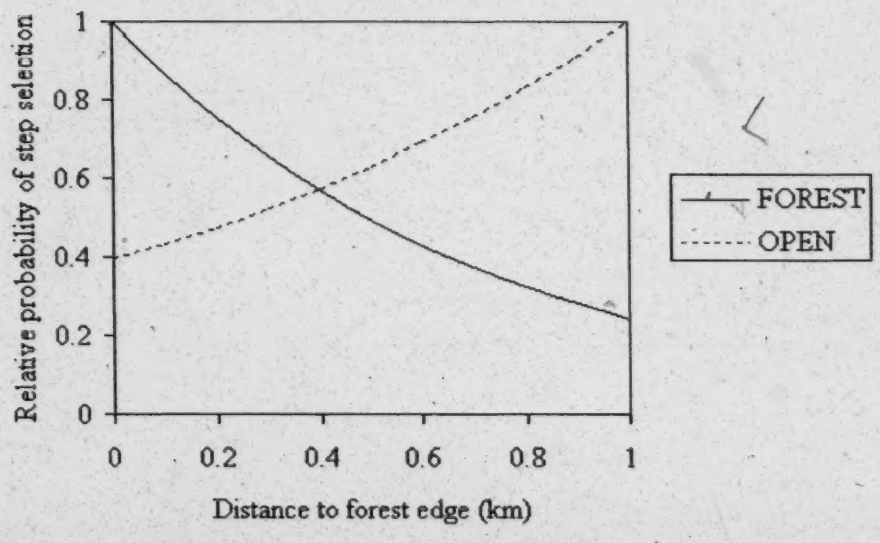


Figure 3.6. Relative probability of a step being selected by an elk at dawn (a) and dusk (b) given the mean distance to a forest edge along the step, as calculated from the step selection function (SSF) models provided in Table 2.1. At dawn, steps in open habitats are more likely to end closer to the forest edge, and steps in forested habitats are more likely to end further from the forest edge. This is consistent with elk transitioning from open to forested habitats at dawn. The selection patterns are reversed at dusk, which is consistent with elk transitioning into open habitats at dusk.

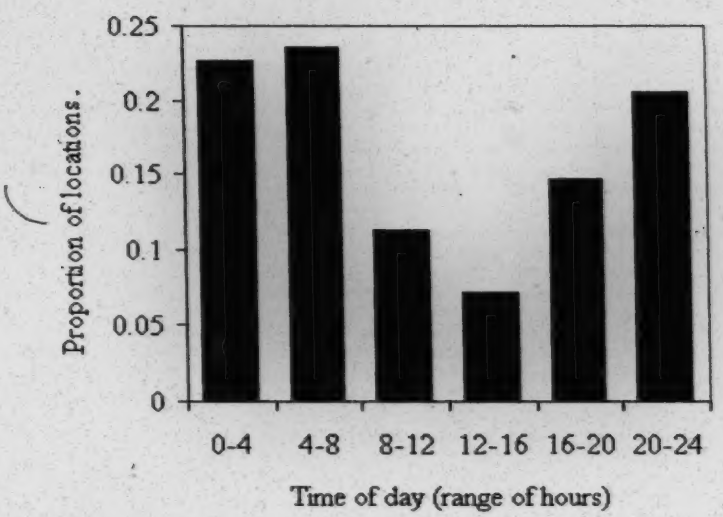


Figure 3.7. Proportion of elk locations falling within 100m of sampled willow sites that occurred within 6 time-of-day periods.

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CHAPTER 4

GENERAL DISCUSSION AND CONCLUSIONS

To demonstrate that a trophic cascade is occurring between wolves, elk and willow on the northern range we must demonstrate that elk browse negatively affects willow growth and that wolves affect the intensity of browsing on willow. We have shown that browsing reduces stem growth, but because we do not have historical data on intensity of browsing at our sites we can only address how wolves affect browsing intensity indirectly. We did this by examining whether the presence of wolves was a significant predictor of willow growth after accounting for hydrological, topographic and climatic factors that also influence growth. For both species of willow (*Salix boothii* and *S. geyeriana*) the presence of wolves on the landscape was a significant predictor of growth.

Given the possible direct and indirect effects that could mediate a trophic cascade, we suggest that there is little evidence to suggest that direct effects could be a significant mechanism at this point in time. The movement models described in Chapter 3 are consistent with the hypothesized behaviourally mediated trophic cascade between wolves, elk and willow on Yellowstone's northern range. However, to develop a better mechanistic understanding of a trophic cascade that is mediated by indirect effects of wolves on elk it will be necessary to quantify the relationship between predation risk, group size, distance to hiding cover, willow patch residency time, browse rates and winter severity. While increased predation risk may reduce willow patch residency time (see Abramsky et al. 2002) and therefore browse rates, winter severity is likely to have

the opposite effect as elk become more willing to visit risky habitats to meet their energy requirements. Predation risk also appears to influence group size (Creel & Winnie 2005), which may affect willow browse rates if patch residency time changes as a function of group size. Behavioural studies are needed to characterize the complex interplay of these factors.

The term "natural experiment" has been used to describe the reintroduction of wolves into Yellowstone because it has provided researchers with the opportunity to examine the consequences of re-establishing a top predator into an ecosystem as though it were a treatment in an experimental design. However, "experiment" is misleading because three important elements of a true experiment were absent: randomization, replication and control. Of course in practice it is virtually impossible to manipulate ecosystems in an experimental design and we must capitalize on these natural experiments when they arise. However, rather than relying on statistical evidence to guide our conclusions as in a true experiment, in the case of natural experiments we must consider the overall weight of evidence. The results presented in this thesis support the hypothesis that a trophic cascade between wolves, elk and willow is mediated by indirect effects of wolves on elk on the northern range.

While ecologists have largely been preoccupied with studying the direct effects of predation on prey populations (Messier 1991, Boutin 1992, National Research Council 1997), for community conservation the indirect effects of predators may be the most significant (Schmitz 1998, Soulé et al. 2003, Pickett et al. 2005). In this context, understanding these effects is a directive for advancing ecosystem conservation and biodiversity maintenance (Berger et al. 2001, Soulé et al. 2003). Our results suggest that

predator restoration has resulted in community-altering effects, and in the longstanding debate over Yellowstone's northern range dynamics, the effects of wolf restoration on communities may prove to be an endorsement of the use of ecological process for conservation (Carroll et al. 2001).

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